ON THE OCCURRENCE AMONG ECHINODERMS OF LARVÆ WITH CILIA ARRANGED IN TRANSVERSE RINGS, WITH A SUGGESTION AS TO THEIR SIGNIFICANCE.

CASWELL GRAVE.

In this paper a short account is given of some observations made at the laboratories of the United States Fish Commission at Woods Hole and Beaufort on the larvæ of various echinoderms. The attempt is also made to show that these observations, taken together with those made by other students of the group, have a direct bearing upon one phase of the problem of the early ancestry of the echinoderms.

It would be quite impossible to give an intelligible discussion of the bearing these observations are interpreted to have upon this subject without first recalling the hypotheses which have been put forward by other students of the group to account for its origin and present organization.

The hypothesis which now seems to have the most general acceptance is not the work of any one mind but represents the work of many. It would be difficult, therefore, in giving a hasty review of its most important points, to credit each of its authors with just his contribution, so I shall make only such comments in passing as will serve to explain the changes and additions which seem to me to be warranted.

OBSERVATIONS.

Holothurians.

The barrel-shaped pupæ of Holothurians have been long known, having been described by Müller,[1] Semon [2] and others. They arise in each case by the breaking up and rearrangement of

[1] J. Müller, "Abhandlungen über die Larven und Metamorphose der Echinodermen," *Abl. Kgl. Akad. Wiss. Berlin.*

[2] R. Semon, "Die Entwicklung der Synapta digitata, und die Stammesgeschichte der Echinodermen," *Jena Zeitschr.*, Vol. XXII., 1888.

the ciliated bands of the fully formed auricularian larvæ at the time when the metamorphosis into the adult form is about to take place. Semon's figures of the auricularian larva and the pupa

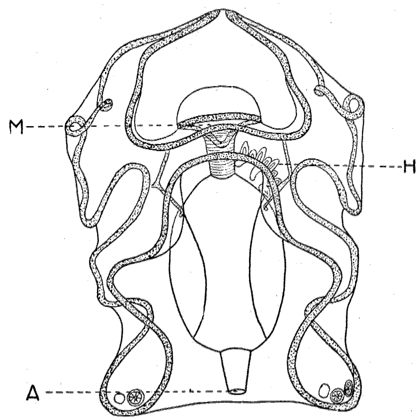

FIG. 1. Auricularian larva of *Synapta digitata*. After Semon. *M*, mouth ; *H*, hydrocœle ; *A*, anus. The ciliated bands stippled.

of *Synapta digitata* are reproduced in outline in Figs. 1 and 2. During the pupal stage the mouth shifts from a ventral to a terminal position and the tentacles and tube feet first become functional.

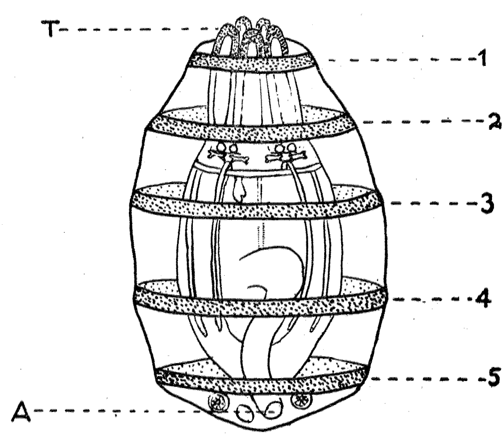

FIG. 2. Pupa of *Synapta digitata*. After Semon. *A*, anus ; *T*, tentacles ; 1, 2, 3, 4 and 5, ciliated rings.

The ciliated rings of the pupa are five in number and are arranged transversely to its long axis.

Selenka[1] has studied and figured the larva of *Cucumaria doliolum* which, although totally unlike an auricularian larva, can be well compared with a pupa. It is an elongated free swimming creature with four, sometimes five, transversely arranged ciliated rings, in addition to which, at the anterior end, there is a ciliated field. This ciliated field is one of the first of the larval structures to disappear as development progresses. In Selenka's figure of this larva, reproduced in outline in Fig. 3, five tentacles and two

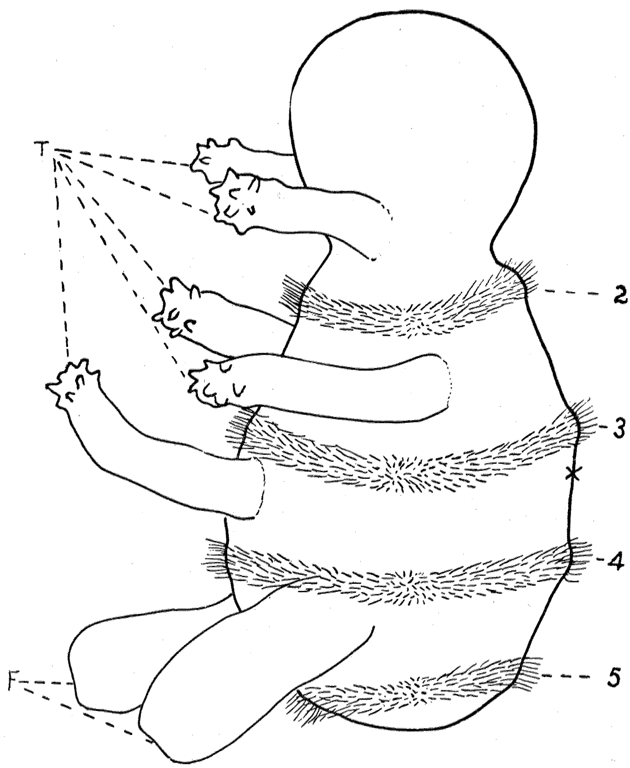

FIG. 3. Larva of *Cucumaria doliolum*. After Selenka. *F*, tube feet; *T*, tentacles; 2, 3, 4 and 5, ciliated rings.

tube feet are shown to be developed and the rotation of the mouth and tentacles to the terminal position has begun. The eggs of *C. doliolum* are quite large and well supplied with yolk,

[1] E. Selenka, "Zur Entwicklung der Holothurien," *Zeit. f. wiss. Zoöl.*, Vol. XXVII., 1876.

thus differing widely from the small transparent eggs of *Synapta digitata.* The efficient locomotor and feeding apparatuses with which the larva of the latter species is provided, enabling it to care for itself, are not needed by the larva of *Cucumaria doliolum* for whose care provision has already been made. The larva of *Cucumaria* can, as it were, give its whole attention to the production of a creature with the structure of the adult while the larva of *Synapta* must make this secondary to food getting.

Crinoids.

In *Antedon rosacea,* the only species of crinoid the development of which has been studied, the eggs are supplied with considerable yolk and for a time the developing larvæ are brooded.

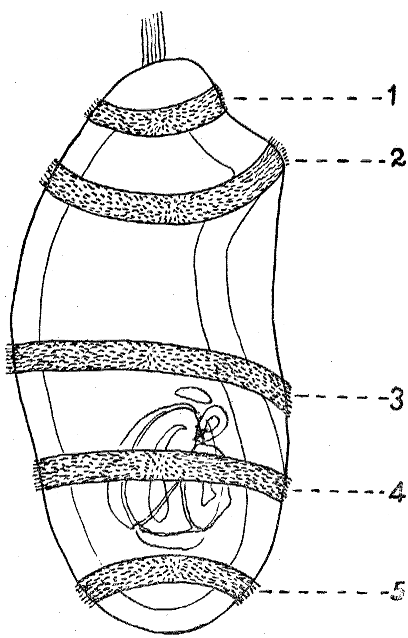

FIG. 4. Larva of *Antedon rosacea.* After Seeliger. Internal organs shown in posterior end. 1, 2, 3, 4 and 5, ciliated rings.

The free-swimming period is of short duration and the development is more or less direct. The larva is elongated and cylindrical and is encircled by five transverse ciliated rings. An

apical tuft of longer cilia is also present. Seeliger's[1] figure of it is reproduced in outline in Fig. 4. No pore canal is developed at this stage but the point on the hydrocœle at which it will appear later, I have indicated by a small x.

Ophiurids.

For a long time the larvæ mentioned above were the only observed cases in which the ciliated bands are arranged in transverse rings, and they were considered to have no special significance. Since 1899, however, I have found three other cases

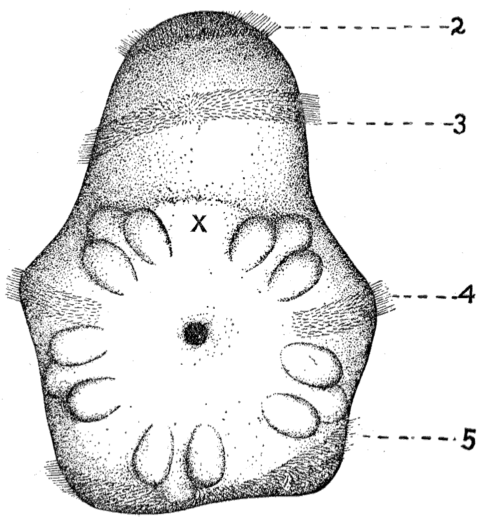

FIG. 5. Ventral view of the young larva of *Ophiura brevispina*. Original. 2, 3, 4 and 5, ciliated rings.

which exhibit the same peculiarity and which represent two other classes of echinoderms.

The larva of *Ophiura brevispina*, which I[2] described in 1899, is well supplied with yolk and very early in its development it sinks to the bottom and clings to grass blades where it undergoes its late larval stages and final metamorphosis. It is a larva without arms or processes of any kind and no skeletal rods such

[1] O. Seeliger, "Studien zur Entwicklungsgeschichte der Crinoiden," *Zoöl. Jahrb.*, Bd. VI., 1892.

[2] Caswell Grave, "Ophiura brevispina," *Mem. Natl. Acad. Sci.*, 1900.

as are found in ophiuran plutei are developed, although at one time I mistook the beginnings of the skeletal plates of the adult for such. The anterior end of the larva is produced into a long preoral lobe about which two ciliated rings are developed. The posterior end is enlarged and contains the various internal structures of the larva and developing ophiurid. The mouth is ventral and interrupts the third ciliated ring of the larva (numbered 4 in Fig. 5). The fourth ring (5) surrounds the posterior end. The dorsal pore is situated at the point indicated by the small x between ciliated rings 3 and 4. As development progresses the preoral lobe diminishes in size until finally it is entirely ab-

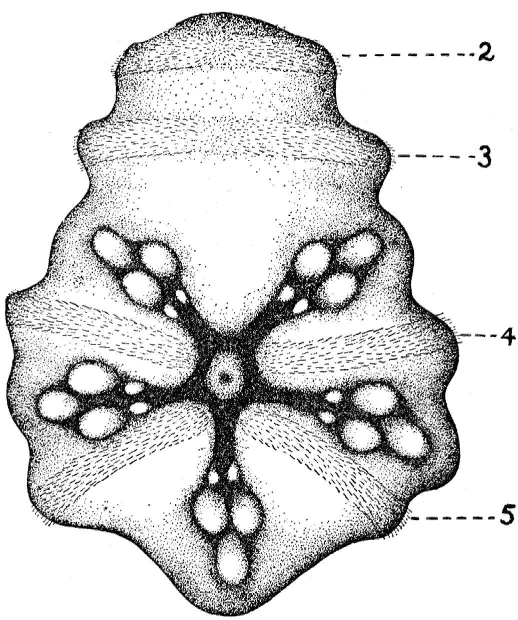

FIG. 6. Older larva of *Ophiura brevispina*. Original. The change in position which takes place in the ciliated ring (5) is shown.

sorbed. During late larval life a change in the arrangement of one of the ciliated rings also takes place. The ring numbered 5 becomes interrupted on the ventral side and takes on a more definite relation to the mouth (see Fig. 6).

In 1900 I found a second ophiuran larva at Beaufort which, in its metamorphosis from the pluteus to the radial form, showed the

same tendency to rearrange the ciliated bands into transverse ciliated rings which is found among the holothurians. The outline of the pluteus is shown in Fig. 7. When the developing ophiurid has become quite large and the tissues of the pluteus are being absorbed, the ciliated bands of certain of the arms become applied to the disc in a quite definite manner, viz., about the madreporic interradius which had an anterior position in the larva, a complete ring is formed; an interrupted ring is laid down between rays 5 and 4 on one side and 1 and 2 on the other. A third ring crosses the base of ray 3. Not until I had examined a

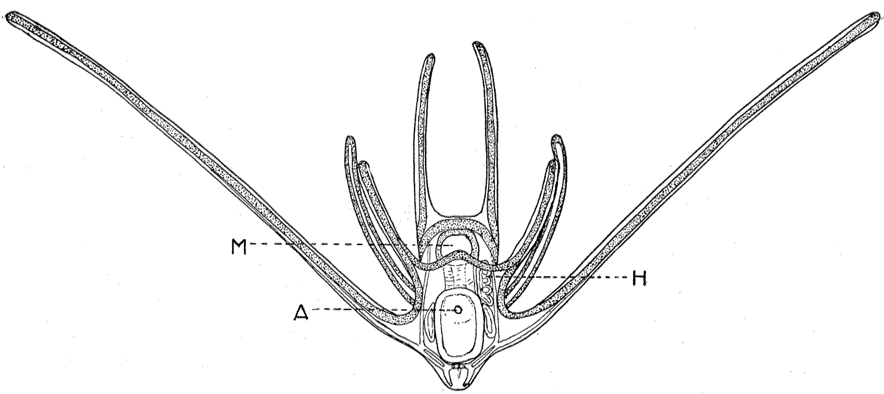

FIG. 7. Ophiuran pluteus (sp.?) from the "tow" at Beaufort. *A*, anus; *M*, mouth. *H*, hydrocœle. Ciliated bands stippled.

number of these metamorphosing plutei was I satisfied that this arrangement of the ciliated areas was not accidental but in all cases examined (a dozen or more) the arrangement was practically the same as that shown in Fig. 8.

Echinoids.

During the summers of 1900, 1901 and 1902 I succeeded in rearing large broods of the larvæ of *Mellita testudinata* from the fertilized egg to the form in which the adult structure is attained. The larva is a typical highly specialized pluteus as will be seen from the outline of Fig. 9. The just metamorphosed *Mellitas* all showed three parallel transverse ciliated rings; the middle one of which is interrupted by the mouth (see Fig. 10). The function of these ciliated rings in the young *Mellitas* is probably to

assist them in feeding until the tube feet have grown sufficiently to assume the function.

The Hypothetical Bilateral Ancestor.

Although numerous papers have been written on the subject of the phylogeny of the echinoderms there are but few which retain their vitality at the present time. In these, notwithstand-

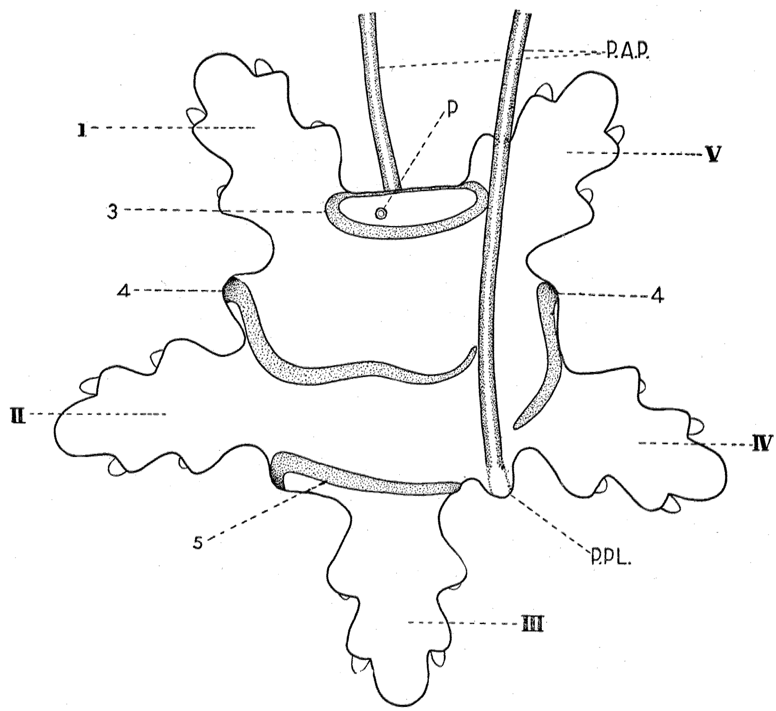

FIG. 8. Outline of the young ophiuran which metamorphoses from the pluteus shown in Fig. 7. Original. I., II., III., IV. and V., arms of the ophiuran; 3, 4 and 5, ciliated rings. *P. Pl.*, remnant of the posterior end of the pluteus. *P. A. P.*, long posterior arms of the pluteus which are never absorbed but are finally dropped. *P.*, madreporite.

ing the fact that many differences in detail exist, there is a very great similarity in the views set forth and I may state in this connection that the facts of this paper and many of my unpublished observations are an additional support to the hypothesis which has been gradually developed by Bury, McBride and

Bather, and serve to carry it one step further. Each of these students has reconstructed the hypothetical ancestor both in its bilateral free swimming stage and the stage during which it became radially symmetrical. The same plan is followed in this paper.

The papers of Bury,[1] McBride[2] and Bather[3] in which the hypothetical bilateral ancestor of the echinoderms is reconstructed and figured, are so well known and the reasons for every detail of the anatomy of the creature are therein so well set forth that it would be a waste of the reader's time to again do more than give an outline of the supposed structure of the hypothetical organism, discussing such points only in which a change is made.

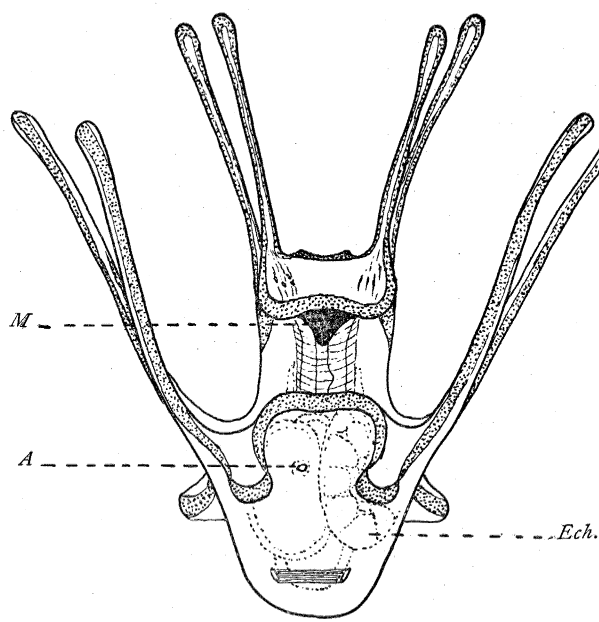

FIG. 9. Pluteus of *Mellita testudinata*. Original. *A*, anus; *Ech.*, developing sand dollar; *M*, mouth. Ciliated bands stippled.

[1] Henry Bury, "The Metamorphosis of Echinoderms," Q. J. Mic. Sc., No. 149, 1895.

[2] E. W. McBride, "The Development of Asterina Gibbosa," Q. J. Mic. Sc., No. 151, 1896.

[3] F. A. Bather, "A Treatise on Zoology." Part III., "The Echinoderma." Edited by E. Ray Lankester, 1900.

Briefly then, the earliest ancestor of the group of echinoderms of which there is much trustworthy evidence, was a free-swimming organism of microscopic size with an elongated body and a long preoral lobe. At the tip of the preoral lobe a sense organ and

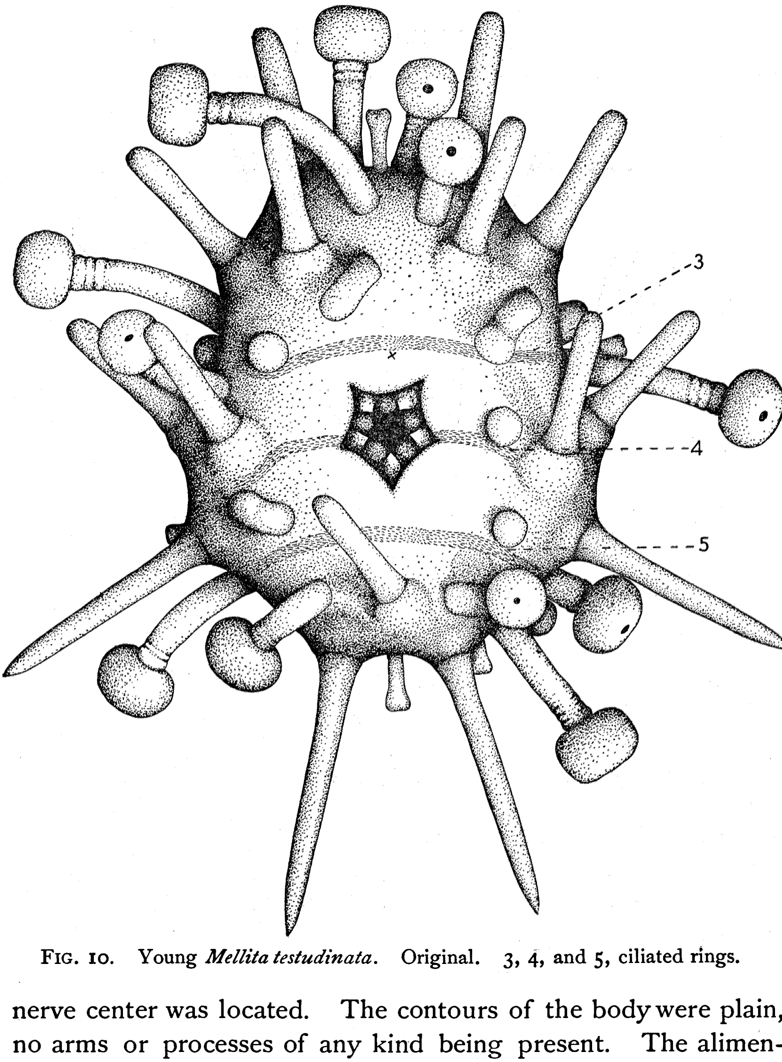

FIG. 10. Young *Mellita testudinata*. Original. 3, 4, and 5, ciliated rings.

nerve center was located. The contours of the body were plain, no arms or processes of any kind being present. The alimentary tract occupied the posterior part of the body, the mouth and anus opening ventrally. Three pairs of body cavities, arranged symmetrically with reference to the alimentary tract, were present.

The anterior pair extended into the preoral lobe where it may have been united into a single cavity. Posteriorly its cavities were placed on the right and left of the œsophagus and each cavity opened to the exterior, on the dorsal surface of the animal, through a ciliated duct. The posterior end of each anterior cavity was connected with the corresponding cavity of the middle pair by a second duct, also ciliated. The middle cavities were situated on either side of the point of union of the œsophagus and stomach. The posterior cavities were larger than those of the anterior and middle pairs and were applied to the stomach, forming a mesentery on the dorsal mid line.

If Fig. 11 *a*, of this paper is compared with Bury's Fig. 45, McBride's Fig. 157 and Bather's Fig. 1 it will be seen that the general plan is the same with differences in detail only.

Bury's idea that the hydrocœle (left middle body cavity) encircled the œsophagus (the right cavity having entirely disappeared) even during the period of the free-swimming existence of the animal, is, in the light of recent observations, an unnecessary assumption and one for which no explanation has been made. The changes which take place in the *posterior* pair of body cavities of echinoderm larvæ, by which the *left* one becomes horseshoe-shaped and encircles the stomach, are almost exactly similar to those by which the *left middle* body cavity takes on the form of a ring surrounding the œsophagus. If to explain the former it is necessary, as Bury and others believe, to assume a shifting of the position of the mouth and œsophagus incident to a life on the bottom, then a similar explanation for the latter is also called for. I agree with the more recent writers in the assumption that both the hydrocele and left posterior body cavity acquired their circular shape and position around the alimentary canal, at the same time, viz., during the period when the entire organization of the animal was being readjusted to its new conditions of life on the bottom.

According to McBride's hypothesis, each of the middle body cavities possessed, during the free swimming stage of the ancestor, five tentacles which were used in the capture of food. There is good evidence for the existence of two hydrocœles (middle body cavities), as McBride has shown in his work on

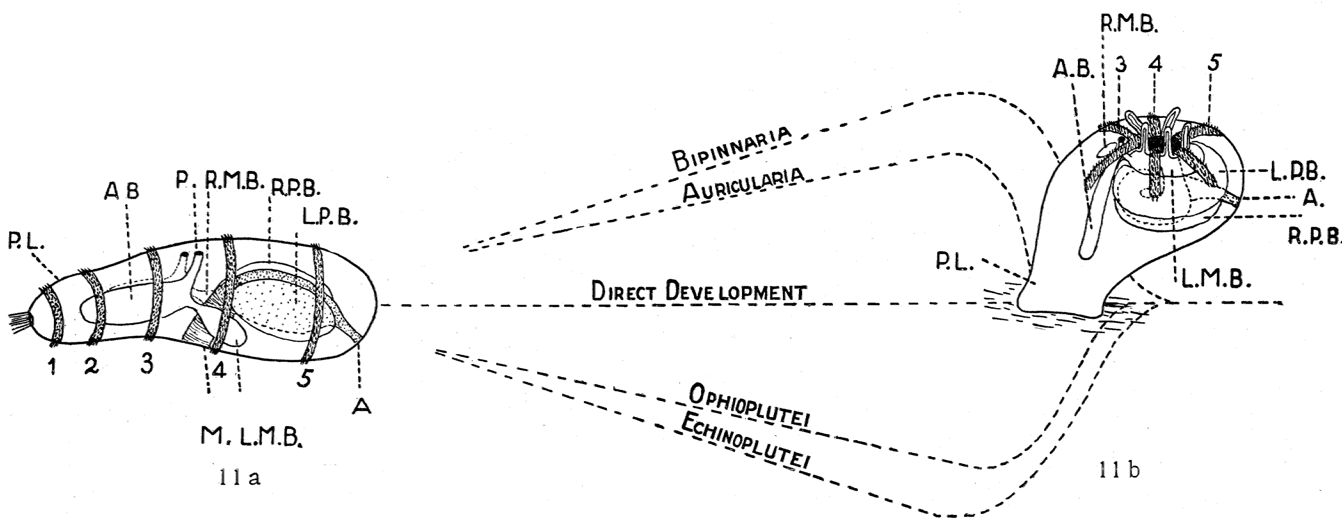

Fig. 11. Scheme to illustrate the suggestions of this paper concerning the struture and appearance of the hypothetical free-swimming and fixed ancestors of the echinoderms and the relation which the type of development of the more familiar echinoderm larvæ bears to the type which is represented by the larvæ of *Antedon*, *Cucumaria* and *Ophiura*. 11*a*, the hypothetical free-swimming ancestor. 11*b*, the hypothetical fixed ancestor. *A*, anus; *A.B.*, anterior body cavity; *L.M.B.*, left middle body cavity (hydrocœle); *L.P.B.*, left posterior body cavity; *M*, mouth; *P.*, dorsal pore; *P.L.*, preoral lobe; *R.M.B.*, right middle body cavity; *R.P.B.*, right posterior body cavity; 1, 2, 3, 4 and 5, ciliated rings.

Asterina, and as is further demonstrated in the pluteus of *Mellita*, but that they possessed tentacles or assisted in capturing food *at this time* is not, I think, supported by evidence. The structure and function of the left hydrocœle as an organ of locomotion and feeding was, in my opinion, acquired during the period of sedentary life after the animal had so increased in size that ciliary action alone was not equal to the work of food gathering. This point will be more fully discussed, however, further on.

To the bilateral ancestor as above described I would add, in the place of the general coat of cilia with which it is usually provided, a locomotor and feeding apparatus consisting of five transversely-placed ciliated rings and an apical tuft of sensory cilia. The position of each is shown in Fig. 11, *a*.

Semon[1] in his discussion of the larva of *Synapta digitata* concludes that the transverse ciliated rings of both the holothurian pupæ and the larva of *Antedon* are to be considered as secondary structures. Lang[2] also states that it is not at all likely that the ciliated rings (of echinoderm larvæ) have any phylogenetic significance. From the facts then available this was the only conclusion warranted and its has been accepted almost without exception by zoölogists. It seems to me however that the observations recorded in this paper, which have been made since the publication of the works of the authors just mentioned, make it worth while to again call attention to the question and to discuss the bearing which the accumulated facts have upon our conception of the structure and history of the hypothetical pelagic ancestor of the echinoderms.

Larvæ such as *Auricularia*, *Bipinnaria*, *Brachiolaria* and *Plutei* have never, to my knowledge, been seriously consided to be primitive although the attempt to establish a relationship between echinoderms and *Balanoglossus*, on account of the general similarity of the movements and external characters of the *Auricularia* and *Tornaria* larvæ, comes very near to an implied belief in their primitiveness. In each of the above-mentioned larvæ we

[1] Richard Semon, "Die Entwicklung der Synapta digitata und die Stammesgeschichte der Echinodernen." *Jena Zeitschrift*, Bd. XXII., 1888.

[2] Arnold Lang, "Text Book of Comparative Anatomy," p. 546. (Eng. trans.)

have to do with highly specialized organisms, there being a long period in the life of each during which it is thrown upon its own resources. Its existence during this period depends upon its ability to procure food and escape from its enemies. The rigorous selection which must take place under these conditions can not have failed to have had a profound effect upon the whole organization of the larvæ and especially upon their external characters.

The whole tendency has been however to look for primitive characters among free-swimming larvæ, throwing aside those which are brooded or otherwise cared for as much more likely to be modified and secondary. If my suggestion as to the significance of the larvæ of echinoderms with transverse rings is correct then this view is incorrect. On the other hand we would expect to find the least modified development among larvæ which are freed, to a greater or less extent, from the task of caring for themselves, provided in such cases the eggs have not been so crowded with nutritive materials as to become greatly enlarged or that, during the brooding, no connections with the mother are established or protective structures developed. Kenogenetic characters are no doubt found in both types of larvæ and the problem is to ascertain which has remained truer to the ancestral form.

The final, sudden and complicated metamorphosis into the adult form which is so characteristic of *free-swimming* larvæ is good evidence that they have been carried far out of the path of phylogeny. In larvæ without a long independent existence the metamorphosis is gradual and such as might be expected if it is in any way a true picture of the past history of the race.

No very great similarity is shown in the external forms of the familiar types of echinoderm larvæ and it is difficult to think of any one of them as having been the type from which the others originated, but it is possible to think of them all as having arisen from a type of larva such as is found in *Antedon*, *Cucumaria* and *Ophiura*.

Owing to the similarity in position of the ciliated rings with reference to the other organs of the body of the larvæ of the above-named species, and all other cases in which ciliated rings

have been found, a very definite homology can be shown to exist between them, as I have endeavored to indicate by the numbers which have been placed opposite the rings in each of the drawings. It is conceivable that the long arms of *Auricularia*, *Bipinnaria*, and the various *plutei* may have arisen and been developed from elevations of the ectoderm beneath certain parts of the ciliated rings, the result of which would have been an increase in their length and thereby an increase in their efficiency in locomotion and feeding. The relation which the type of directly developing larvæ of *Antedon*, *Cucumaria* and *Ophiura* is suggested to bear to the familiar types, is shown in Fig. 11; the larvæ with transverse ciliated rings being considered the primitive condition from which the other larvæ have been specialized and carried far out of the path of phylogeny, as a result of their independent life. To this type of development the specialized larvæ tend to return at the time when their free-swimming life is given up for one on the bottom, as is indicated in holothurian pupæ, a certain ophiuran larva and young *Mellitas* in all of which the transverse ciliated rings reappear at the time of metamorphosis in the form in which they were of functional importance to the common ancestor during the early period of its life on the bottom.

All larvæ have not deviated to the same extent from the direct line, as is shown not only in their less complicated structures but also in the less radical readjustment of organs which takes place during their metamorphosis. In ophiurid plutei, for example, the larval mouth and œsphagus are taken over as such into the adult form, which, as has been pointed out, must have been the case in phylogeny. In echinoid plutei, however, the specialization which has taken place in these organs has been carried so far that it is impossible to readapt them to the needs of the adult and new ones must be formed.

The Attached Form and the Origin of Radial Symmetry.

With almost no exception, students of the embryology and anatomy of the echinoderms see no other way, at present, to account for the peculiar asymmetry of certain of the organs and

the perfect radial symmetry of other structures, which are characteristic of the adult condition and which arise, in every known case, by the remodelling of the structures of a larva which is bilateral in its entire organization, than by assuming that the group has been derived from a bilateral pelagic organism, similar to the one described above, which at a very remote period in its existence exchanged its free swimming life for one on the bottom during which it became fixed.

Briefly stated, the steps by which the present organization of an echinoderm are generally accounted for, and for which there is more or less evidence, are as follows: Pelagic life was given up for one on the bottom because of less competition and a greater food supply in the latter place. The preoral lobe became gradually modified into an organ for fixation. The mouth, at first directed downward as was its position in pelagic life, gradually moved to the left until it took up a position in which it was directed upward. This, in a fixed animal, feeding upon microscopic organisms, is its most favorable position as is shown by its position in animals which exist at present under these conditions. During the migration of the mouth and œsophagus, those organs of the left side which would obstruct such a movement (left middle and posterior body cavities) were carried along and each became drawn out into the shape of a horseshoe and greatly hypertrophied. In the final position of each, the opening of the horseshoe was directed anteriorly. The middle and posterior body cavities of the right side also became changed in position and correspondingly reduced in size. The left middle body cavity retained its connection with the exterior through the greatly reduced anterior left body cavity and its duct, but the duct of the right side disappeared. During this period when food was plentiful and easily accessible and when no energy was used in locomotion, a rapid increase in the size of the creature took place and radial symmetry was developed. There is such a diversity of opinion, however, as to the details of this process that I will attempt to give but one; that which has been suggested by my own observations.

The ciliated rings were useful to the free-swimming animal not only as organs of locomotion but were used in feeding as well,

and during the period when it was fixed on the bottom certain of the rings continued to function as food gatherers. The two rings which encircled the preoral lobe, being purely locomotor in function, were lost, but the other three took up a more definite relation to the mouth and formed six paths for conducting food to it (see Fig. 11, *b*). The retention of the ciliated rings among directly developing larvæ and the return to a condition with ciliated rings among larvæ which possess a more complicated ciliated apparatus during their free-swimming life may, as I have stated elsewhere, be explained on this ground. The entire number of rings is not in every ease retained or reproduced because two, Nos. 1 and 2, belonged entirely to the locomotor apparatus (preoral lobe) and except in the holothurians and crinoids (for reasons suggested later) are no longer needed. Only those rings are retained which in the ancestral line had a function in feeding, and which are needed for the same purpose during the metamorphosis of the larvæ themselves until the developing tube feet are ready to assume the function.

This ciliated feeding apparatus which had been brought over by the hypothetical fixed echinoderm from its free-swimming condition and which, in the new surroundings, had, at first, answered every need in this line, became gradually inadequate to furnish it, as it increased in size, with enough food. Those portions of the ciliated sensory epithelium of the mouth situated between the ends of the ciliated paths were then gradually developed into tentacles into each of which a diverticulum of the left middle body cavity, lying below, protruded (see Fig. 11, *b*). In the anterior space only, did no tentacle develope. This space contained the external opening of the left middle body cavity (madreporite), the left anterior body cavity (*Ampulla*) and possibly the reproductive organ. There was hence no space in which a sixth tentacle might have developed.

In this way the pentamerous structure of the hydrocœle may be accounted for and I assume, with others, that the hydrocœle formed the basis upon which the entire radial symmetry of echinoderms was built. The ciliated tentacles, simple at first, branched as they grew in length and assumed more and more the function of food collecting. As the animal increased in size the space

immediately surrounding it failed to yield a sufficient supply of food. The tentacles in reaching about over the bottom in search of more, detached the animal and a crawling habit was developed. As the tentacles grew in length and complexity a like development in the organs which nourish, enervate, support and protect them would naturally follow. The tentacles being five in number, we have in them a possible origin for the pentamerous symmetry which characterizes the nervous and skeletal systems and a considerable part of the cœlomic cavities of all echinoderms. At the time when fixed life was given up by the ancestor of those echinoderms which are at present free living, each of its radii probably contained a five-branched tentacle, since this is the number which is possessed by many echinoderms at the period when their metamorphosis is being completed. The period of fixation was long enough and the changes which took place in the organization of the animal at this time were so great that all trace of an *anterior* or a *posterior* part, as such, was lost and now, in its second period of free life, the direction of locomotion depends wholly upon external conditions.

During the period when the common ancestor of the group was fixed, differentiations into at least three different types took place. One line is now represented by holothurians, one by crinoids and another by asterids, echinoids and ophiuroids. Among crinoids alone the fixed condition has been retained. In this group the problem of enlarging its base of supplies was solved not by becoming free but by the elongation of the organ of attachment, and by the migration of the mouth and tentacles still further toward the opposite end. In the type which has given rise to holothurians, the mouth and tentacles migrated in just the opposite direction, *viz.*, into the organ of attachment and were thereby brought into relation with the bottom. The free-crawling habit was later acquired. The ancestor of the starfishes and sea-urchins made no permanent use of its organ of attachment and no further migration of the mouth took place but it was brought into direct relation to the bottom by the rotation of the body as a whole.

ZOÖLOGICAL LABORATORY OF THE JOHNS HOPKINS UNIVERSITY,
April, 1903.